DIVERSE NODAL TYPES IN RHODODENDRON

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RHODODENDRON IS ONE of the largest of the angiosperm genera. In spite of obvious diversity in habit, flower form, and many other characters, there is little doubt that the group is a natural one. The only serious reservation to this view is that the three species forming the subgenus THERORHODION might be better regarded as a distinct genus (Sleumer, 1949). Proposals to subdivide the genus in recent years have been based on expediency in the face of such large numbers rather than on botanical merit (Copeland, 1943).

It might be expected, therefore, that studies of the range of form shown by various features of *Rhododendron* would reveal interesting examples of diversity within a coherent group. This is the first in a series of investigations into the anatomy of the genus. Here the anatomy and development of the nodes of foliage leaves and cataphylls is considered.

Previous studies by others have brought to light striking examples of such diversity. Maximowicz (1870) defined subgenera by the relationships between floral and vegetative buds. Sinclair (1937) demonstrated two well-defined types of vegetative bud, and Cowan (1950) published a detailed survey of trichome types within the genus. Kingdon-Ward (1947) makes some further suggestions, especially concerning characters of the seed. Hayes et al. (1951) thoroughly investigated the anatomy of the leaf blade and discussed its relation to the subdivisions of the genus.

In 1914 Sinnott demonstrated that three types of node occurred in dicotyledons, and that in many families one type only was found to be present. He also noted several families in which more than one type of node was present, and further examples have been recorded, e.g. Icacinaceae (Bailey & Howard, 1941), Epacridaceae (Dormer, 1945; Watson, 1967), Monimiaceae (Money, Bailey & Swamy, 1950), Escalloniaceae (Swamy, 1954). These findings did not seriously affect the importance of the node in classification, because different nodal types usually were found to correspond to major subdivisions within a family.

The need for comparisons to be made between appendages of similar age was brought out by Swamy (1949), working with *Degeneria*, who found that the complexity of the node might increase as successive leaves formed in the seedling. Canright (1955) found a similar ontogenetic sequence in members of the Magnoliaceae. Bailey (1956) also compared the nodes of seedlings and mature shoots and found that while sequences from the unilacunar to the tri- or multilacunar condition were frequent the reverse transition was not observed. This limitation is generally of little significance when the foliage of mature woody plants is being compared, though the work of Kato (1966, 1967) shows that variation may

occur between successive nodes of some genera. Work by Müller (1944), Philipson (1948), and Post (1958) also demonstrated the need for considerable caution in comparing nodal types in herbaceous plants. For example, in *Helleborus foetidus* L., Müller found mature foliage leaves to possess seven to eleven traces, but this number diminished in higher leaves until bracts with a single trace were reached. Post found uni-, tri-, and multilacunar nodes in the genus *Frasera*, with reduction series up the appendages of the flowering stem. In the related *Swertia perennis* L. the multilacunar nodes diminished in complexity upwards, and also downwards in the basal cataphylls.

Records of different nodal types within one genus of woody plants are few. Pellegrin (1908) records tri- and unilacunar nodes in *Genista*, and Saha (1952) tri-, bi-, and unilacunar nodes in *Citrus*. The Araliaceous genus *Pseudopanax*, with most species multilacunar, has at least one trilacunar species (Philipson, 1965) and the South American members of *Griselinia* are trilacunar whereas the New Zealand species are pentalacunar (Philipson, 1967).

The occurrence of the five types of node here described in the mature foliage of a genus of woody plants is therefore of interest. Their relationship with other characters which have been used in the classification of the genus is discussed in the last section of this paper.

SCOPE AND METHODS

This investigation is concerned principally with the pattern of the vascular supply to mature foliage leaves. The node and petiole have been examined in 264 species, as listed in the last column of the APPENDIX. These were selected from all the subdivisions of the genus recognized in Sleumer's "Ein System der Gattung *Rhododendron*, L." (1949), as modified by him (Sleumer, 1958 and 1964), as well as from all the series and subseries recognized in the *Rhododendron Handbook*, Part I (Synge, 1963).[1] Subsidiary observations relate to the development of these patterns during the growth of the primordium and also to the acquisition of the mature pattern in successive leaves of seedlings. The nodal patterns of other lateral appendages (cotyledons, bud scales, and perulae) have also been examined.

A series of hand sections at right angles to the main axis was made to determine nodal types. For a few selected examples of each nodal type, tangential and radial series of longitudinal sections were also cut to clarify the interrelations of the traces. Petioles were sectioned, always at the base and mid-point, but often also distally. All these sections were stained in an aqueous solution of aniline sulphate and mounted in glycerine jelly.

[1] Throughout the text the classification proposed by Sleumer has been used, but where it has been necessary to refer to smaller units the subseries of the Handbook have been employed. *Therorhodion* (Series *Camtschaticum*) was investigated as most authors have included it in *Rhododendron*. Authorities for specific names of Rhododendrons are omitted from the text but appear in the APPENDIX.

THE NODE OF THE MATURE FOLIAGE LEAF

The patterns of vascular supply to the foliage leaves fall into five types as follows:

I. Simple Unilacunar Node (FIG. 1)

The simplest type of node found consists of a single trace which departs from the stele of the axis leaving a single gap. The vascular supply
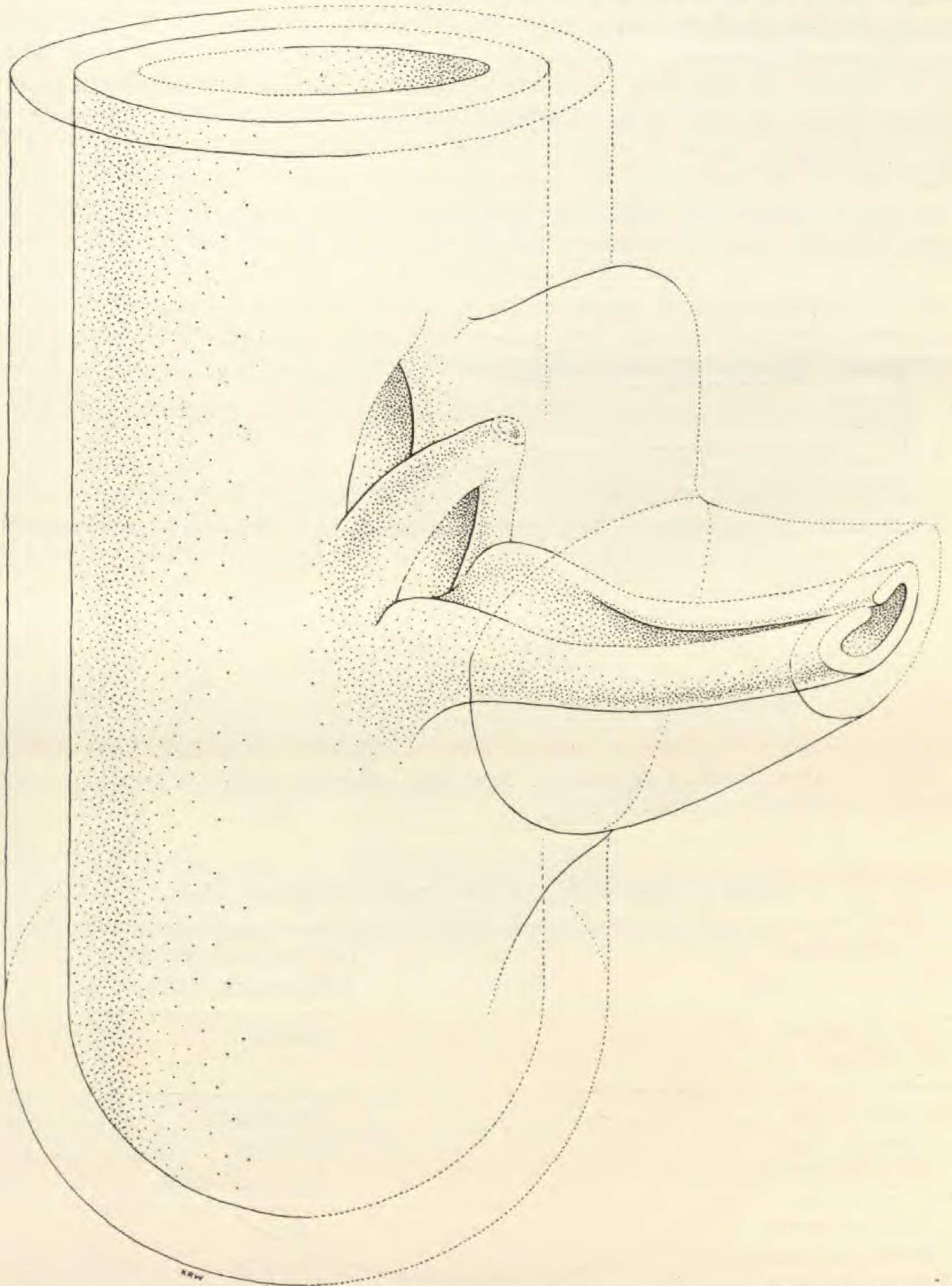

FIG. 1. SIMPLE UNILACUNAR NODE (semi-diagrammatic). The single leaf trace and the bud trace depart from one gap.

normally continues across the cortex and into the petiole as a single unit and remains unbranched as far as the base of the lamina. Rarely, lateral branches may occur as the petiole approaches the lamina. Such branches have been observed in *Rhododendron camelliaeflorum, R. tsangpoense, R. maddenii*, and *R. scabrifolium*.

This simple type of node, or slight modifications of it presently to be described, occurs in all the 136 species examined from the groups listed in TABLE 1. These groups comprise approximately 55 percent of the species in the whole genus.
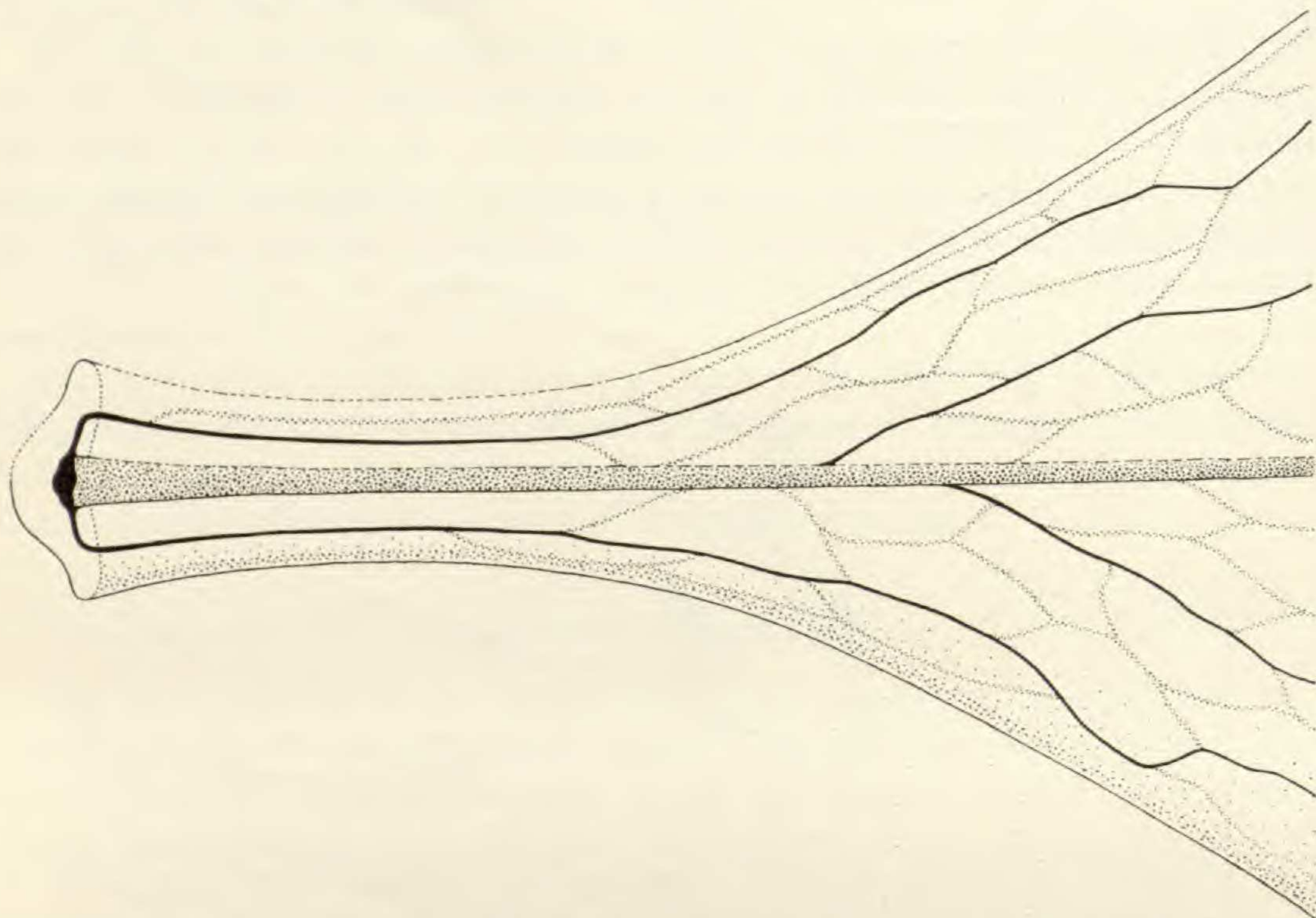

FIG. 2. *Rhododendron albiflorum*. Leaf base, showing origin of two accessory bundles outside the abscission layer.

TABLE 1. **Distribution of the Simple Unilacunar Node**

SUBGENERA (Sleumer's system)	EQUIVALENT SERIES (Handbook, 1963)
PENTANTHERA TSUTSUTSI	Azalea
AZALEASTRUM (except Sect. CHONIASTRUM)	Albiflorum Ovatum Semibarbatum
RHODORASTRUM PSEUDORHODORASTRUM RHODODENDRON PSEUDAZALEA	All the "lepidote" Series

Modifications of this simple type occur in a small proportion of the species. The variants fall into a number of categories, which are summarized below.

a) The leaf trace branches in the proximal half of the petiole, or near the abscission layer (Fig. 2). Examples are listed in Table 2.

b) The leaf trace divides into separate strands while still in the cortex of the axis. These subdivisions reunite after passing the abscission layer. This fragmentation of the leaf trace into distinct strands which form an arc is very clearly developed in *R. nuttallii* and occurs in some other large-leaved members of Maddenia and Vireya, but not in all. In very large leaves of *R. nuttallii* one or two bundles may remain as distinct strands in the petiole for some distance, even as far as the mid-point, but they eventually merge into the central bundle. The leaf trace is fragmented into distinct strands in leaves examined of the following species of Vireya: *R. intranervatum, R. javanicum, R. brookeanum, R. lowii, R. crassifolium*, and *R. retivenium*. However, some species of this section with very large leaves were found to have very little, if any, fragmentation. Examples are *R. superbum* and *R. leucogigas*.

c) The accessory branches in the petiole originate from the stele of the axis independently of the central leaf trace. This condition was observed in one leaf of *R. schlippenbachii* and applied to the accessory on one side only. The other accessory arose, as in other leaves of this species, as a branch of the central trace. This particular node, therefore, was bilacunar.

d) Small adaxial strands of vascular tissue accompany the petiole bundle (Fig. 3). This was observed in species of the subsection Maddenia belonging to subseries *Ciliicalyx* (*R. johnstoneanum*) and *Megacalyx* (*R. lindleyi, R. megacalyx* and *R. nuttallii*).
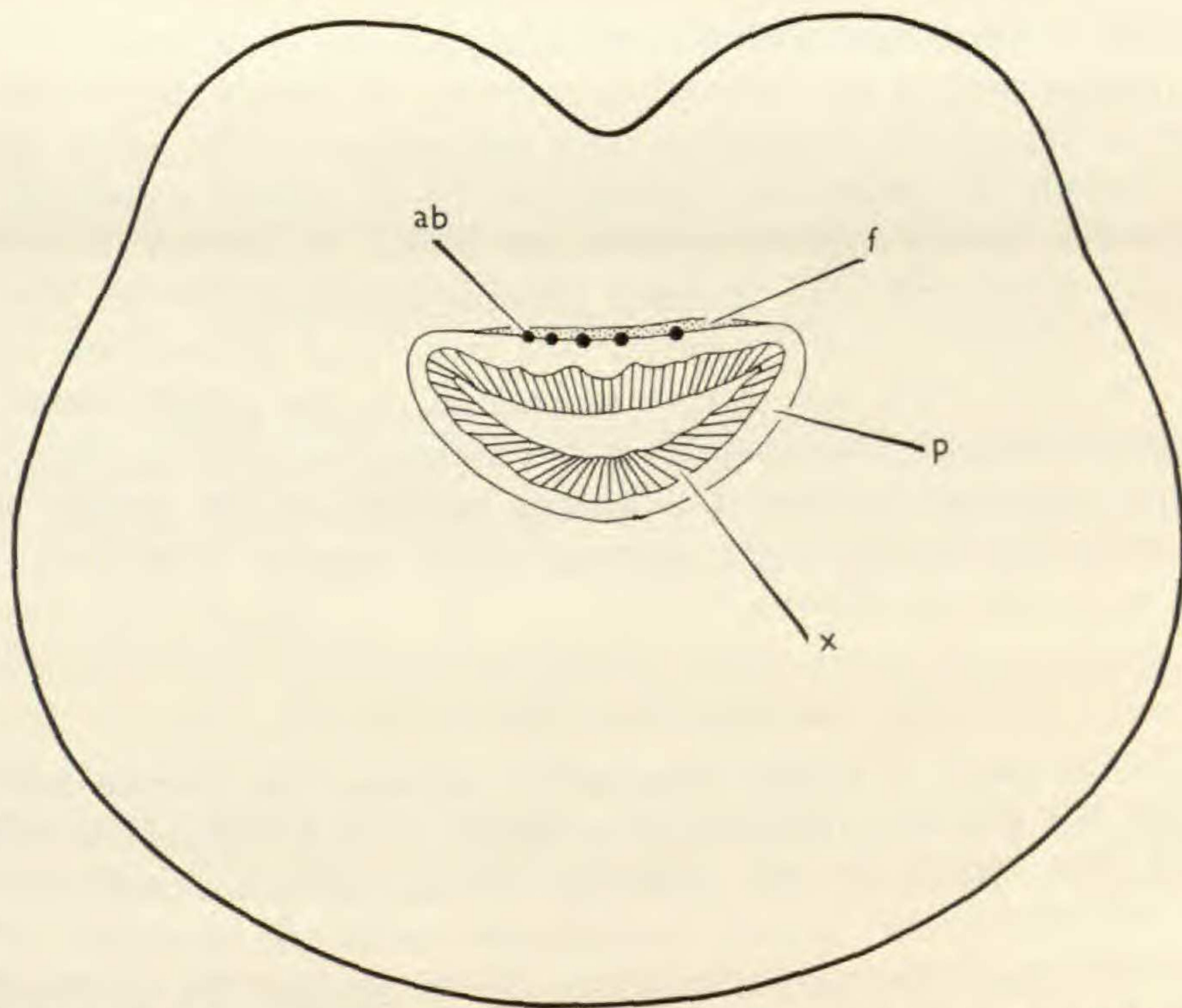

Fig. 3. *Rhododendron megacalyx.* Transverse section showing adaxial bundles in petiole. *ab*, adaxial bundles; *f*, fibers; *p*, phloem; *x*, xylem.

TABLE 2. **Simple nodes with accessory bundles**

GROUP	SPECIES	REMARKS
BOOTHIA	*sulfureum*	branches at base, or mid-petiole, or unbranched
PHAEOVIREYA	*superbum*	branches at base
PSEUDOVIREYA	*invasiorum*	branches near base
SOLENOVIREYA	*jasminiflorum*	branches near base
EUVIREYA		
BUXIFOLIA	*commonae*	branches at base
JAVANICA	*culminicolum*	branches at base
	leucogigas	branches at base
CANDIDASTRUM	*albiflorum*	branches at base
VISCIDULA	*nipponicum*	branches at base
PENTANTHERA	*luteum*	branches at base
	occidentale	branches near base
BRACHYCALYX	*schlippenbachii*	branches at base
TSUTSUTSI	*yedoense*	branches near base
	kaempferi	branches at base in sucker shoots: normal foliage unbranched

A review of these modifications indicates that the occurrence of branch traces (accessories) is not unusual in azaleas. Although this condition is not rare in VIREYA, it occurred in only one species of the other lepidote groups, namely *R. sulfureum*, though not in all leaves examined. The largest leaves among lepidote species are found in Section VIREYA and Subsection MADDENIA, and in both groups fragmentation of the trace occurs. In MADDENIA subdivisions of the trace may persist well into the petiole. In that event the transverse section of the petiole bears a resemblance to that of more complex nodal types (see below). This resemblance is superficial because the lateral bundles in the petiole always reunite with the central bundle, whereas in the complex type they remain distinct and enter the lamina.

II. Intermediate Node (FIG. 4)

In general there is a clear distinction between the simple node just described and the more complex type found in *Rhododendron* subgenus *Hymenanthes.* However, the nodes of all the species examined of the section CHONIASTRUM (series *Stamineum*) exhibited features of both these nodal types. Because of the difficulty in placing the CHONIASTRUM node, it was felt that its aberrant nature was best emphasized by referring it to a separate type, here designated the Intermediate Node. The
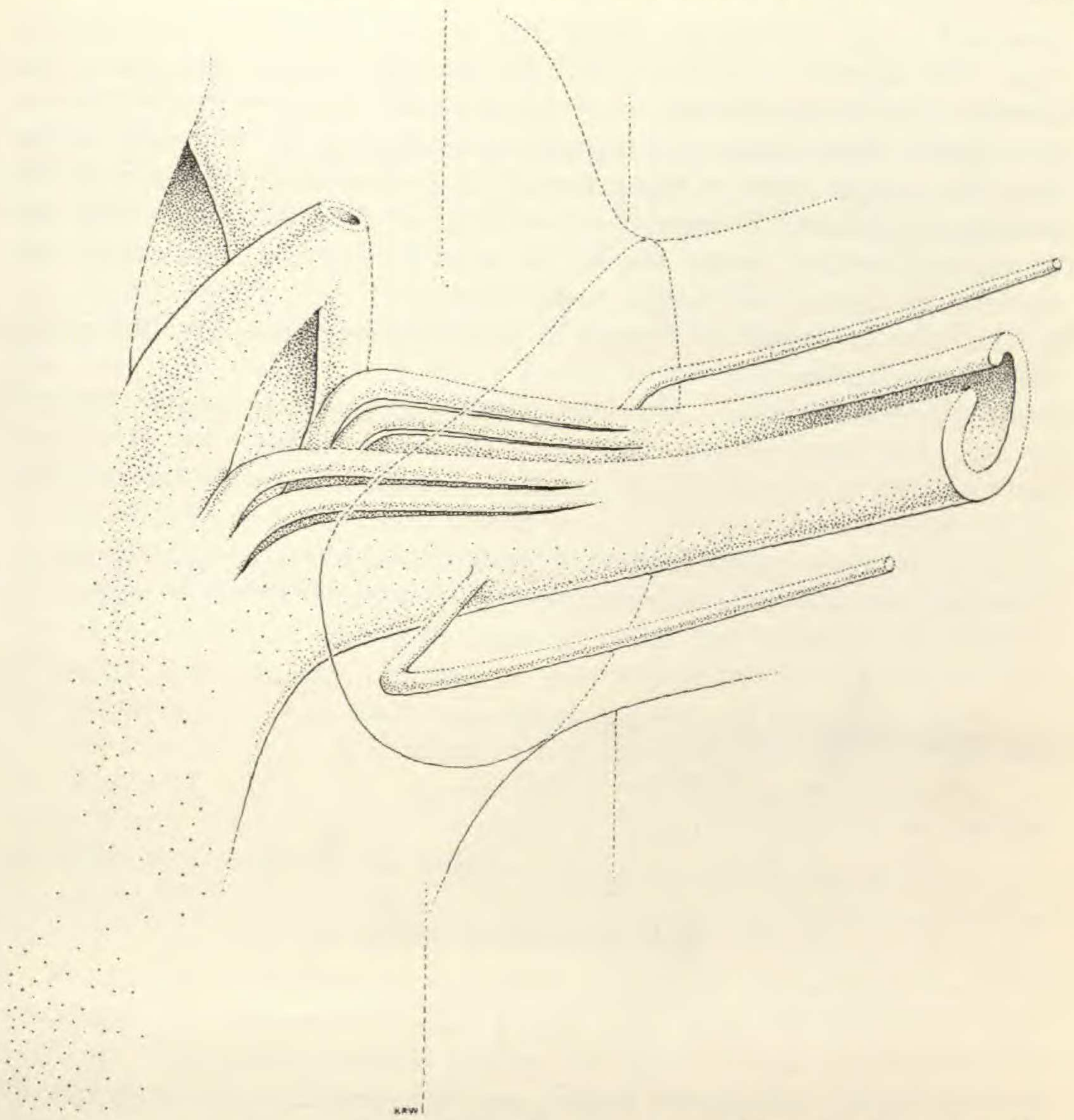
FIG. 4. INTERMEDIATE NODE (semi-diagrammatic). While in the cortex the leaf traces are closely aggregated into a central cylinder. In the petiole these traces unite to form a central strand to each side of which is an accessory bundle.

recognition of the peculiarity of this nodal type appears to be justified, as the section CHONIASTRUM has been considered aberrant within the genus on several grounds (see, for example, Kingdon-Ward (1947) on fruit and seed characters).

In nodes of this type, the leaf trace, which arises from a single gap in the stele, is composed of a number of bundles (typically five) at the level of the abscission layer. These soon unite to form a central arc-shaped strand within the petiole. Immediately outside the abscission layer accessory bundles arise from this central strand and follow a course parallel to the abscission layer before turning along the petiole.

The above description would apply almost as well to the Complex Unilacunar Node to be described below. However, it is considered that the CHONIASTRUM node (invariably present in all species of this section

examined — see APPENDIX) would be wrongly placed in the complex type. This opinion is based on the fact that the separate portions of the central trace do not diverge, as in the typical complex type, but remain throughout their course as a compact arc. And again, this node differs from the simple type in the presence of accessories together with the division of the central trace. It is of interest that this small, very aberrant and natural group displays a vascular pattern which does not conform to any of the major nodal types.

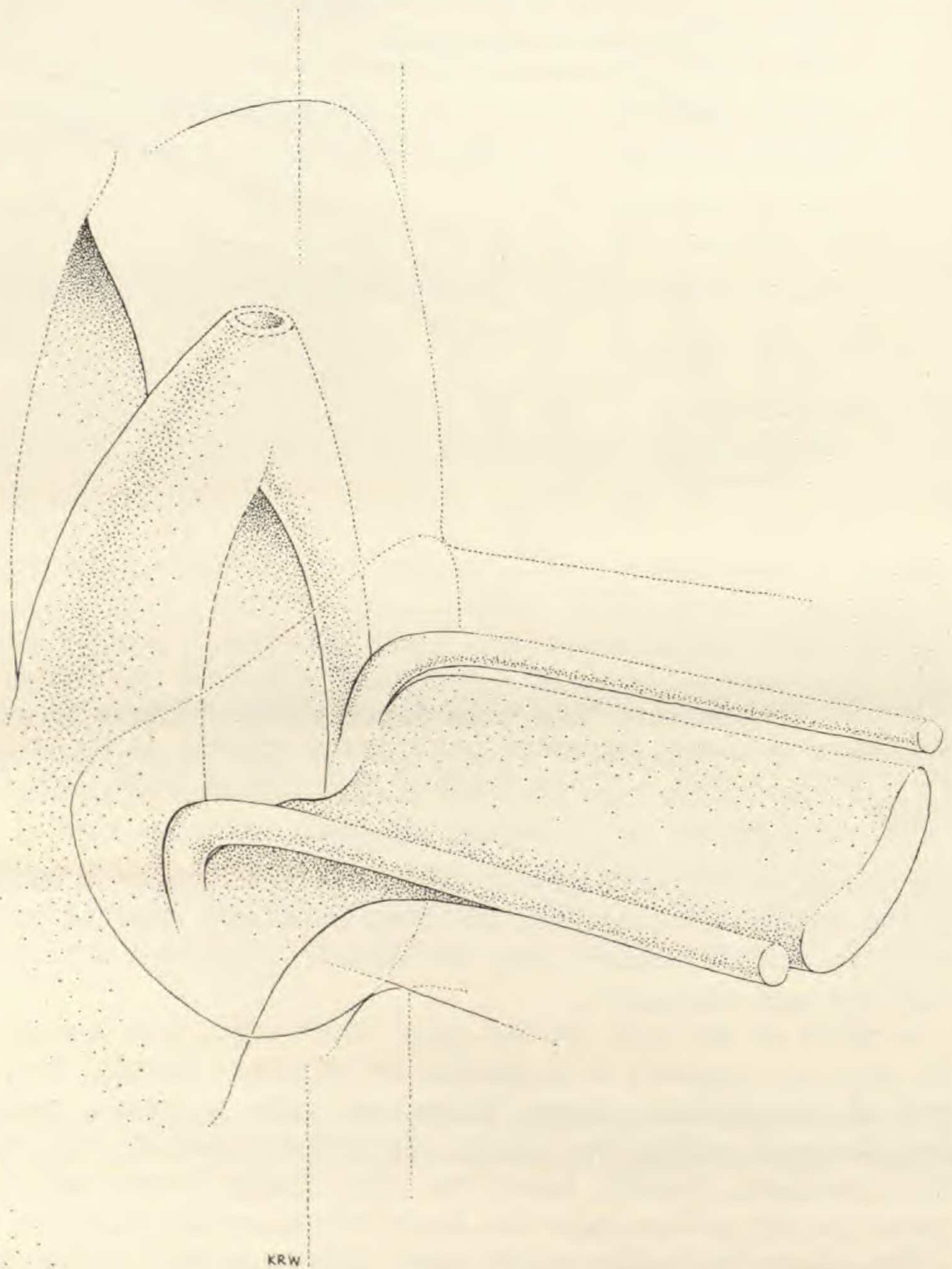The term Intermediate is used in a descriptive sense, without phylogenetic implication.

FIG. 5. THREE-TRACE UNILACUNAR NODE (semi-diagrammatic). Three strong traces diverge from a single gap.

III. Three-trace Unilacunar Node (Fig. 5)

The foliage leaves of *Rhododendron camtschaticum* are borne on lateral shoots which arise from buds situated below the terminal inflorescence buds. These terminal buds open to reveal shoots which bear a small number of flowers. Each flowering branch is subtended by a large leafy bract somewhat different in shape from the foliage leaves. Both the bracts and the foliage leaves are characterized by a type of leaf trace distinct from that of all other species examined. The nodal structure varies in detail, but the most distinctive form is found in the leafy bracts where three strands diverge from a single gap in the stele. These traverse the cortex and enter the petiole separately. The mid-trace is larger than the two laterals, but these are noticeably stronger than the accessory bundles found in the petioles of many Rhododendrons. In foliage leaves a single arc diverges from the stele before dividing into three separate strands (Fig. 5). The point at which the laterals diverge varies considerably, and frequently the two laterals at one node separate from the mid-trace at different distances from the gap. Indeed, in some leaves one or both laterals may not separate until the trace has passed beyond the abscission layer.

This type of node, with three strong traces arising from a single gap, was observed only in the very distinctive species *R. camtschaticum*. Two other closely related species are placed in THERORHODION but no material of these was available for study.

IV. Complex Unilacunar Node (Fig. 6)

In contrast to the simple node, this is a type with a highly complex structure. A number of strands (often five) leave the edge of a single leaf gap. If an axillary bud is present, the upper strands characteristically diverge from the bud trace and may branch during their passage through the cortex. As the strands approach the abscission layer they splay out, often widely, before entering the petiole. Within the petiole the strands converge, uniting to form a large central arc-shaped or cylindrical bundle. Immediately outside the abscission layer accessory bundles arise from this central bundle, as in the Intermediate Node, and follow a course parallel to the abscission layer before turning along the petiole. Alternatively, in species with a very widely splayed central complex, the accessories arise from its lateral extremities without further divergence.

The relationship between the origin of the lateral strands of the central complex and that of the bud trace varies. In many species the laterals diverge from the edges of the bud trace (Fig. 7, a); in others they arise from the stele of the axis, and enclose the bud trace (Fig. 7, b). These relationships vary according to the development of the axillary bud and probably also according to the amount of secondary growth which has taken place. Developmental studies will be required to evaluate this feature, but the character of enclosed bud traces was found to be prevalent in certain subsections, notably LACTEA and THOMSONIA.

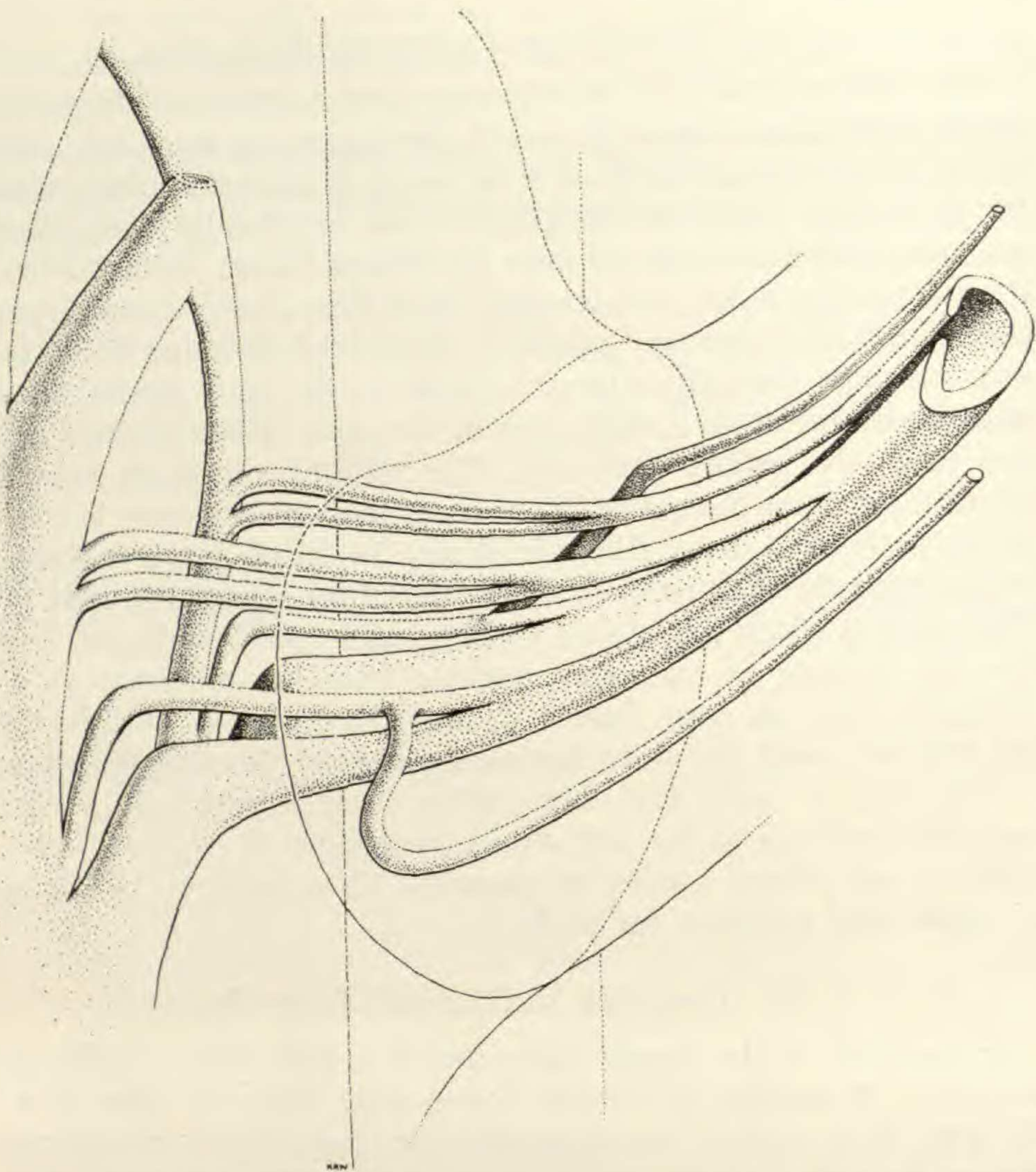Without exception, this Complex Unilacunar Node has been observed

FIG. 6. COMPLEX UNILACUNAR NODE (semi-diagrammatic). Several leaf traces unite to form the central bundle of the petiole, to each side of which is an accessory bundle.

in all subdivisions of the subgenus HYMENANTHES. Indeed, all three previously described nodal types are unknown in this large subgenus. Some variants of the Complex Unilacunar Node are described below, as is the basically similar Complex Trilacunar Node, which is the only other nodal type known in HYMENANTHES.

The species in which trilacunar nodes occur will be considered in the next section. Here some interesting variations of the Complex Unilacunar Node will be described. They are confined to the following subsections.

TALIENSIA. In *R. pronum* (subseries *Roxieanum*) no accessory bundles were present in the petiole. However, the widely splayed and fragmented central strand is very similar to that of *R. gymnocarpum* which is considered to be closely related.

NERIIFLORA. In *R. forrestii* no accessories were observed, though these occurred in the varieties *repens* and *tumescens*. In the lowest foliage leaf of a
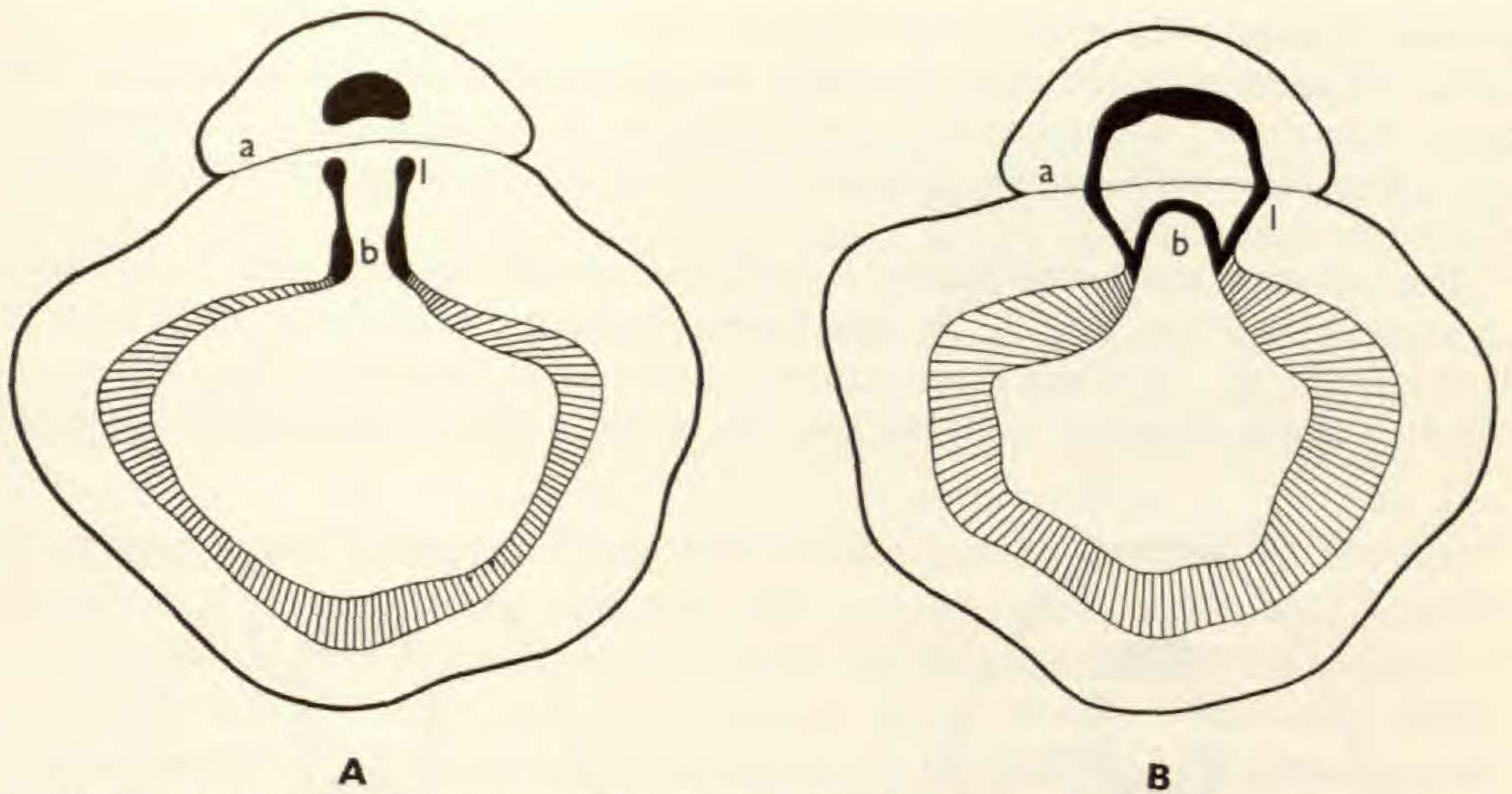
Fig. 7. Relation of lateral leaf traces to bud trace. A, *Rhododendron arboreum*, laterals unite to outer edge of bud trace; B, *R. fulvum*, laterals inserted at inner edge of bud trace (semi-diagrammatic) *a*, abscission layer; *b*, bud trace; *l*, lateral trace of leaf.

branch of *R. sperabile* only one accessory was present, and in *R. neriiflorum* one accessory became weak towards the base of the petiole and made no junction with the central complex. In *R. haematodes* one accessory diverged gradually from the central complex instead of making the usual abrupt departure.

CAMPANULATA. In *R. tsariense* no accessories were present. In a leaf with no axillary bud the central strand was inserted in the gap without obvious fragmentation. This node therefore could be placed in the simple type. However, when buds were present, parts of the central strand arose from the bud trace, a feature which reveals the undoubted relationship of this species. The patterns found in *R. campanulatum* were extraordinarily various. While the typical state of the complex type occurred, in some leaves the accessories failed to diverge from the central complex, arising *de novo* in the petiole base, sometimes with a swollen sheath of dense parenchyma around them. In one example (from seed collected on Mt. Everest by Wilkins, and grown at Dunedin Botanic Garden), most nodes were of the trilacunar type (see below) but one leaf of this plant varied in having only one accessory bundle which did not appear until halfway along the petiole. And again, a leaf of *R. succothii* with only one accessory bundle was found to have a bilacunar node.

THOMSONIA, SELENSIA, CAMPYLOCARPA, SOULIEA. All these related subsections exhibited some variants. The accessory bundles either arose *de novo* outside the abscission layer or diverged from the central complex in the typical manner in *R. campylocarpum*, *R. telopeum*, *R. selense* and *R. wardii*. In *R. dasycladum* and *R. wardii* some accessories diverged gradually from the central strand well above the abscission layer. In some nodes of *R. campylocarpum* one of the accessories arose from a separate gap in the stele, that is to say, such nodes were bilacunar; occasionally the accessory arose *de novo* in the cortex of the stem before continuing through the abscission layer into the petiole. In *R. caloxanthum* the central complex remained as three distinct bundles nearly as far as the mid-point of the petiole. As noted earlier the lateral strands of the central complex characteristically enclose the bud traces in this series, in which case these

bundles appear to be inserted by separate gaps in the stele. This feature becomes exaggerated as further secondary growth occurs. In two species of this series, namely *R. hookeri* and *R. stewartianum* (both subsection THOMSONIA) the nodes were undoubtedly trilacunar, at least in the sense employed in this paper (see next section).

The variation within the species *R. williamsianum* is so great that it warrants separate description (FIG. 8). In some leaves the node was of the typical Complex Unilacunar type; in others no accessory bundles were present in the petiole; in others a single accessory occurred and was either confined to the distal portion
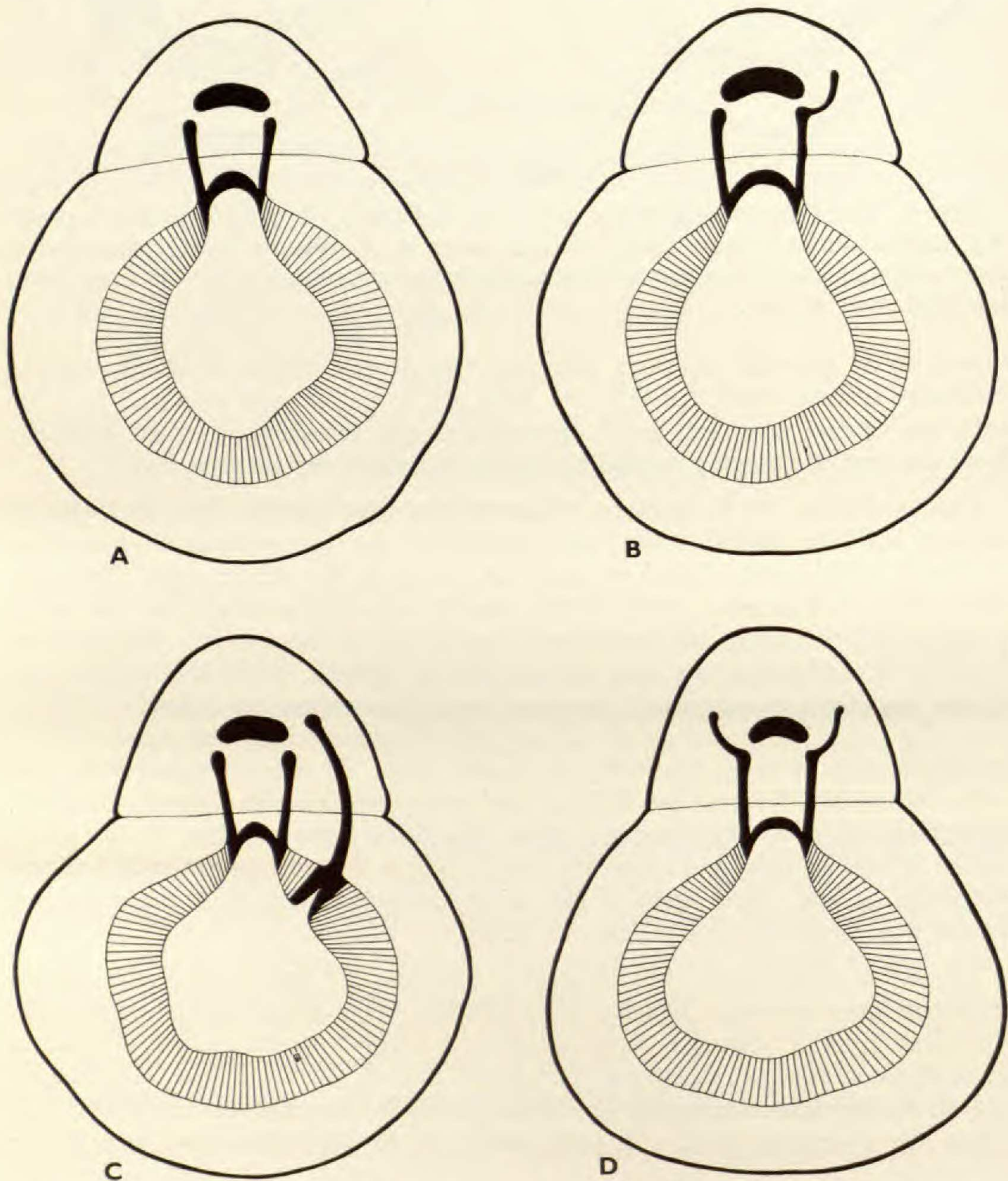

FIG. 8. *Rhododendron williamsianum,* diagrammatic representation of four types of node. A, petiole without accessories; B, petiole with one accessory which fuses with lateral bundle; C, petiole with one accessory which enters stele independently; D, petiole with two accessories, each fusing with its lateral bundle.

only or arose from the central strand at the base of the petiole; while in others the nodes were bilacunar, the accessory arising from a separate gap in the stele.

BARBATA. In one petiole of *R. bainbridgeanum* (subseries *Crinigerum*) only one accessory bundle was present and this diverged gradually from the central complex. Other nodes of the same shoot were normal.

To summarize, the Complex Unilacunar Node is found in all species of the subgenus HYMENANTHES except those with the even more elaborate Complex Trilacunar Node, still to be considered. Considerable variation is found in a few subsections of this subgenus. When accessories are not present this Complex Unilacunar Node can be defined by the complexity of the bundles at the abscission layer. Very rarely this feature may be lacking in leaves without buds, but no species of this subgenus has been found where this complexity never occurs. However, since fragmentation of the central trace occurs in *R. nuttallii* and some species of VIREYA (see above) no absolute distinction can be maintained between the nodal type of the lepidote subgenera as compared with those of the subgenus HYMENANTHES. Nevertheless, these two groups, each with over 400 species can be separated by their nodal structure, almost without exception. The intermediate nature of the node in the section CHONIASTRUM (series *Stamineum*) has been discussed previously. In the subgenus HYMENANTHES only three species were found to lack accessory bundles and in them the central strand becomes divided in at least some nodes. When it is recalled that the node of the subgenera TSUTSUTSI, PENTANTHERA (azaleas) and AZALEASTRUM can also be distinguished from that of the subgenus HYMENANTHES without exception, the taxonomic importance of the node in this genus becomes evident.

V. The Complex Trilacunar Node (FIG. 9)

In several different taxonomic groups within the subgenus HYMENANTHES the accessory bundles in the petiole do not diverge from the central system as in the Complex Unilacunar Node just described. Instead, they arise from strong bundles which leave the stele by independent gaps and link up with the central system just outside the abscission layer. The gaps left in the stele by the origin of these bundles are defined by primary as well as by secondary xylem. The term trilacunar, therefore, is applied to these nodes. However, since all the strands of a leaf trace are included within the same mesh of the original primary pattern of protoxylem, it is perhaps arguable that the pattern is still basically unilacunar. Nevertheless, for comparative purposes this is a most distinctive nodal type, and will be regarded here as trilacunar.

This type of node is characteristic of the subsection GRANDIA where it occurs in all species examined, though not necessarily in all leaves (see below). It also occurs in some species of the following five subsections: BARBATA (*R. argipeplum, R. barbatum, R. erosum, R. exasperatum* and *R. smithii*); FALCONERA (*R. arizelum, R. basilicum, R. falconeri* and *R. hodgsonii*); FORTUNEA (*R. griffithianum*); LACTEA (*R. wightii*), and

THOMSONIA (*R. hookeri* and *R. stewartianum*). The nodes of other members of these five subsections examined (see APPENDIX) were of the complex unilacunar type. In addition, the Complex Trilacunar Node was observed exceptionally in *R. campanulatum*.

An interesting consistent feature distinguishes the trilacunar node of the subsection BARBATA. The strong flanking bundles run horizontally
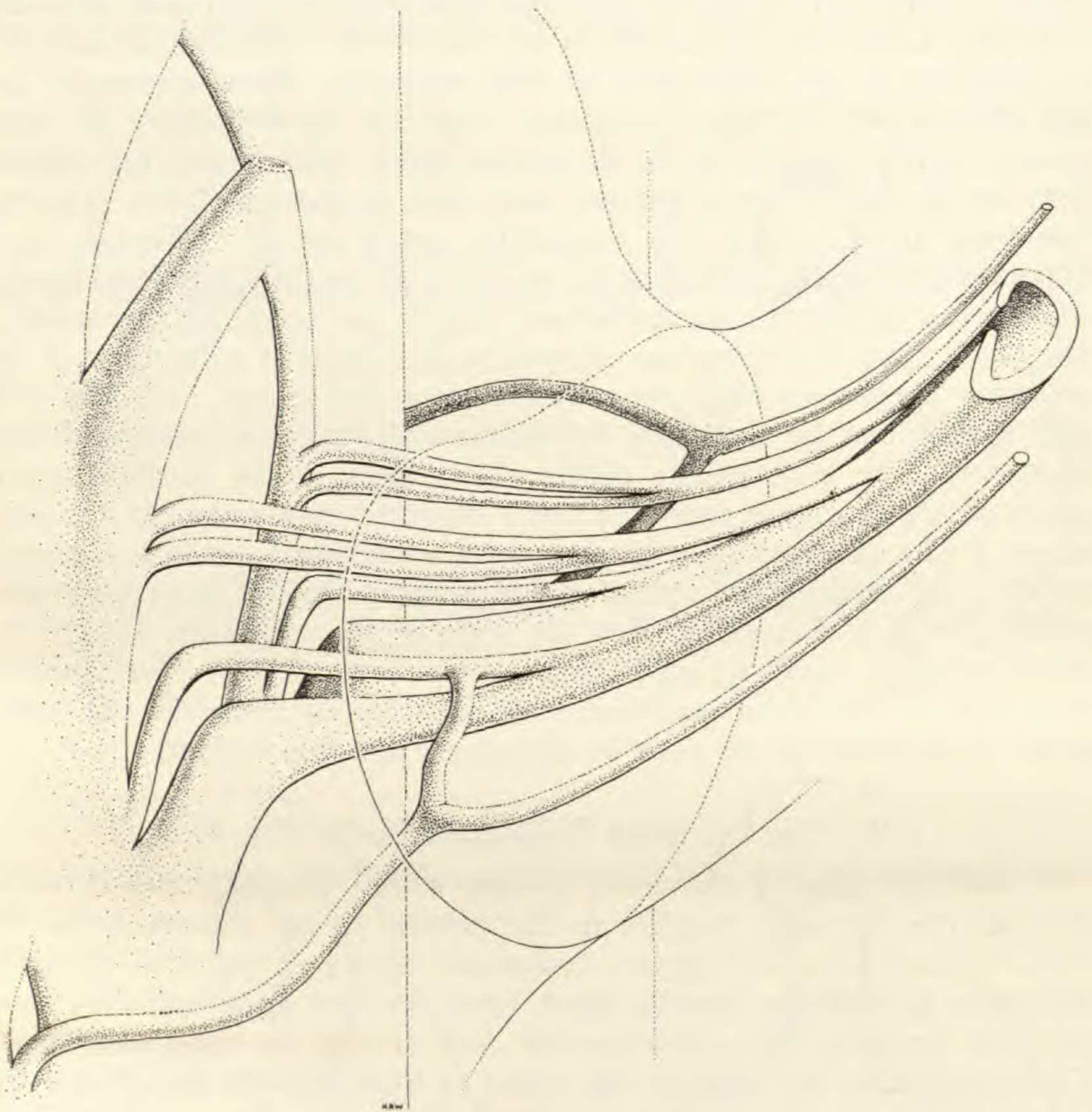
FIG. 9. COMPLEX TRILACUNAR NODE (semi-diagrammatic). Bundles leave the stele by independent gaps and join the central complex in the base of the petiole. From them the accessory bundles arise.

across the cortex, so that their gaps occur higher in the stele than the gap of the midrib. In the remaining groups with trilacunar nodes the flanking bundles arise from gaps some distance below that of the midrib and ascend sharply while crossing the cortex to the abscission layer. The only exception found occurred in *R. basilicum* (FALCONERA) where the node resembles the BARBATA type.

Such complex nodes are subject to considerable variation of detail. In

particularly large specimens of *R. griffithianum* (subsect. Fortunea) and *R. magnificum* (subsect. Grandia), the central complex of bundles is convoluted so that the appearance of a double midrib is produced, and, in the latter, ventral branches of the laterals join the additional ventral fold of the midrib. On the other hand a plant of the Trinwald variety of *R. griffithianum* grown at the Dunedin Botanic Garden had asymmetrical nodes which were bilacunar, and the same condition was found in *R. monosematum* (subsect. Maculifera). Shoots of *R. grande* and *R. griffithianum* had successive nodes which were unilacunar (complex), bilacunar and trilacunar.

In summary, the trilacunar node occurs in some species of five subsections (Barbata, Falconera, Fortunea, Lactea, Thomsonia); occasionally in one species of another (Campanulata); and in all the species examined (though not all the nodes) of the subsect. Grandia.

VI. Nodes of Subgeneric Hybrids

Hybrids between species of the subgenus Hymenanthes and those of other subgenera are rare (Martin, 1963). In view of the distinctive features of the node of Hymenanthes, the nodal patterns of two such hybrids, from species belonging to two subgenera, were investigated. Specimens of *Azaleodendron* (hybrids between species of Hymenanthes and Pentanthera) growing at the University of Canterbury and in the Botanic Garden, Dunedin, were found to have simple nodes similar to those of the subgenus Pentanthera. On the other hand, the hybrid 'Grierdal' (*R.* (subgen. *Hymenanthes*) *griersonianum* × *R.* (subgen. *Rhododendron*) *dalhousiae*), from the Savill Gardens, Windsor Great Park, had nodes similar to those of the subgenus Hymenanthes, that is, of the Complex Unilacunar type.

Two hybrids between the subgenera Rhododendron and Rhodorastrum were provided by the Arnold Arboretum. These were the hybrid 'P.J.M.' (*R. dauricum* var. *sempervirens* × *R. carolinianum*) and another unnamed hybrid (*R. mucronulatum* × *R. carolinianum*). Both were found to have nodes of the simple type. This would be expected as both species belong to subgenera with this type of node.

VARIABILITY IN NODAL PATTERNS

I. Within-plant variation

a. Foliage leaves. Since the principal object of this investigation was to compare the nodes of typical foliage leaves, no systematic study of the variation over the full range of leaf size was undertaken. However, our observations were extensive enough to enable us to conclude that little variation does in fact occur. That is to say, the nodes of plants with characteristically simple nodes are all simple, as would be expected, though some variation in minor features was noted. Similarly, species with complex nodes in general have all their nodes complex, though the greater

scope for variation possibly leads to more frequent modification. A few specific instances of within-plant variation follow, though most have already been mentioned when describing the various nodal types.

R. schlippenbachii. Accessory bundles normally leave the central strand above the abscission layer, but at one node one accessory left the stele by its own gap (bilacunar).

R. kaempferi. Accessory bundles are absent from normal foliage, but in leaves of strong sucker shoots accessories arose at the base of the petiole.

R. grande and *R. griffithianum.* Successive nodes on the same shoot were uni-, bi-, and trilacunar.

R. sperabile and *R. succothii.* Very small accessory bundles are normally present at each side of the petiolar strand. In one leaf only one of these occurred.

R. campanulatum. In one plant, accessory bundles normally branched from the central strand at the base of the petiole, but in one leaf they did not occur until mid-petiole.

R. sulfureum. In one plant, accessory bundles normally arose at the base of the petiole, though they did not all persist as far as the blade. In one leaf these basal accessories were joined by a pair of bundles which branched from the central strand at mid-petiole.

R. williamsianum. In leaves of the same plant accessory bundles may be absent or one may be present. The accessory, if present, may leave the central complex at the base of the petiole or leave the stele by an independent gap.

b. OTHER LATERAL APPENDAGES.

Cotyledons. The cotyledonary node was not investigated in detail. However, the cotyledons of several species of diverse affinity have been examined and all were found to receive a single bundle.

Bud scales. The nodes of the scales which enclose the buds of Rhododendrons are characteristically unilacunar. An exception occurred in a series cut through the scales of a plant of *R. magnificum* which had a very complex pattern of bundles in the nodes of its foliage leaves. The bud scales of this plant had several veins which united with the midrib at the base of the scale: only one bundle entered the axis. In one inner scale, however, a lateral bundle entered the axis independently so that the node of this scale was bilacunar.

Perulae. A feature of many *Rhododendron* leafy shoots is that a terminal group of foliage leaves is separated from the scars of the bud scales by several internodes which bear no foliage leaves. The appendages borne at these nodes are strap-shaped scales, or perulae, which are usually early deciduous, leaving a bare axis below the foliage leaves. In some species, however, these perulae are persistent. The nodes of the perulae were investigated in many species of diverse affinity, including those with the most complex foliage traces, and in all they were found to consist of a single trace. This branches immediately it enters the perula into several parallel veins. A curious feature of these perula-traces is that they are frequently decurrent in the cortex, arising from the stele by gaps as much as 2.5 cm. below the appendage (FIG. 10). The internodes separating the perulae grade from short at the base (i.e. next to the bud-scale scars)
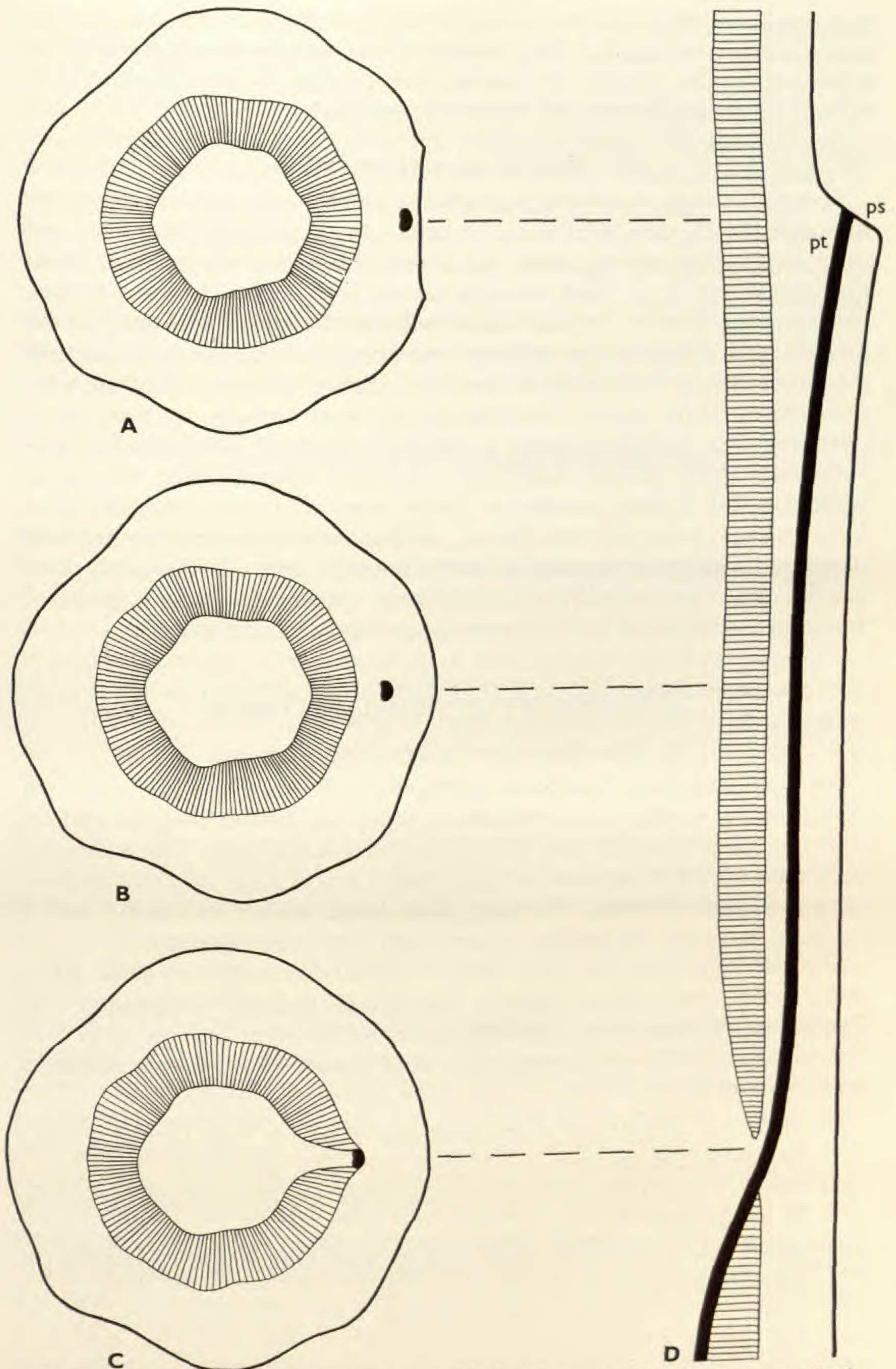
FIG. 10. *Rhododendron magnificum*. Node of perula. A, B, C, successively lower transverse sections at levels indicated on D, longitudinal section. *ps*, scar of perula; *pt*, trace of perula. Secondary xylem hatched, trace in solid black.

to a maximum about three-quarters of the way up the shoot. Above this they decrease in length. The length of the decurrent trace reaches a maximum in the longest internodes, but no simple relationship exists between internode length and degree of decurrence.

II. Within-species variation

Several instances of differences between individuals of the same species were noted. In view of the within-plant variation just described, and since no extensive surveys were undertaken, little can be concluded about the range of variation which may exist among members of the same species. However, the number of species examined, and the great consistency of the findings, with mainly trivial within-plant variation, make it safe to conclude that most species exhibit little variation. Some notable exceptions were encountered, three species standing out as most variable in their nodal structure. The variations noted in different plants of *Rhododendron williamsianum* have already been described and figured (FIG. 8). It is surprising that a species so distinct and so constant in most morphological features as *R. williamsianum* should exhibit such wide variation in nodal structure. The variation may be found between nodes of the same plant and between those of different individuals. Almost as great a range of variation was observed in *R. campanulatum* and *R. campylocarpum*.

DEVELOPMENT OF NODAL PATTERNS

I. Development in Seedling Leaves

An examination of a series of seedlings of the subsect. FALCONERA (in which the mature leaf has a trilacunar node) established that the earliest leaves, ranging in length from 0.7–1.5 cm. were unilacunar. The trilacunar state was reached in the node of a leaf only 2.6 × 1.2 cm. and still without the mature indumentum. However, some longer leaves, between 5 and 7 cm. long and with the mature indumentum were only bilacunar.

One seedling from this same suite of specimens exhibited some interesting nodes intermediate between the simple and the trilacunar state. The leaves did not form a graded series up the stem because their size varied considerably and irregularly. Four leaves in ascending sequence were as follows:

(i) blade 1.8 × 1.25 cm., node bilacunar with one very faint accessory bundle in the petiole;

(ii) blade 0.9 × 0.75 cm., node simple, with one faint accessory bundle in the petiole;

(iii) blade 0.8 × 0.55 cm., node simple, with two accessory bundles in the petiole;

(iv) blade 2.0 × 1.3 cm., node bilacunar with one accessory bundle in the petiole.

In all these nodes the central (or only) trace was undivided. It is of interest to note that the bilacunar and trilacunar conditions arise so

early in the development of the seedling. In contrast to these specimens, seedlings of *R. sinogrande* of comparable size had nodes which were of the Simple Unilacunar type. Leaves with blades 2.0 $\times$ 1.0 cm. showed no sign of accessory bundles in the petiole nor of extra bundles in the cortex. Their only departure from the simple condition was the separation from the central strand of one or two subsidiary traces, which arose in the cortex, passed through the abscission layer, and then reunited with the central strand to form the single bundle of the petiole. In smaller leaves the central bundle remained entire, although the individual vessels could be seen to diverge at the abscission layer. This dilation of the trace as it passes from the stem into the petiole is never observed in typical simple nodes, and can be regarded as the first sign of the development of the complex node of the subgenus HYMENANTHES.

II. Development in the Leaf Primordium

Sections were taken through resting vegetative buds in autumn. The species investigated (*Rhododendron magnificum* and *R. griersonianum*) have mature nodes with Complex Trilacunar and Complex Unilacunar nodes respectively. No time-sequence study of primordia was undertaken, so that the detailed development of the complex node can not be described. The foliage-leaf primordia of both species examined were at an early stage of development with lamina formation only beginning. In each the primordium contained a single procambial strand, representing the midrib, and this was traced downwards until it entered the axis. No rudiment of any other part of the nodal complex was present, thus showing, as might be expected, that the supply of each leaf passes through a simple stage, no matter how complex its final condition may be.

DISCUSSION

The presence within one genus of such diverse nodal structure is, we believe, unique among woody plants. Following the pioneer work by Sinnott (1914), the node was long considered a conservative character, often stable in all members of large taxonomic groups within the dicotyledons. Latterly, this view has been seen to require modification, since considerable variation in nodal structure has been reported within families and even genera (Saha, 1952; Post, 1958). However, until the present time, the unilacunar condition has been regarded as a constant feature of the Ericaceae, although variation has been recorded in the closely related Epacridaceae (Dormer, 1945; Watson, 1967).

The variation in nodal structure observed in the genus *Rhododendron* has been presented here as falling into five types. One of these occurs in a group of three species which have been regarded as forming a distinct genus, *Therorhodion* (e.g. by Sleumer, 1949). We consider that the distinctive nodal anatomy of *R. camtschaticum* provides further evidence for the recognition of this genus. The nodal types found in the

genus *Rhododendron*, ranging from simple to complex, form a natural and coherent sequence into which the three strong, divergent traces of the camtschaticum type have no place.

The remaining four groups fall into two major categories. The Complex Unilacunar and the Complex Trilacunar nodes are clearly very similar morphologically and taken together are found in all the species of the subgenus HYMENANTHES and in no other group. The morphological similarity evident from a comparison of FIGS. 6 and 9 is strengthened by two other considerations. Firstly, these two nodal types may occur together in different species of the same taxonomic group, in different plants of the same species, and even in different nodes of the same shoot. Secondly, a few species with otherwise typical Complex Unilacunar nodes have the lateral parts of the leaf trace inserted so widely that they approach the trilacunar state, or one bundle may clearly enter by its own gap, giving a bilacunar node.

The Simple Unilacunar Node and the Intermediate Node also appear to be linked by similar features. These two nodal types are found in all species of the seven subgenera listed in TABLE I but including CHONIASTRUM. They stand, therefore, in sharp contrast to the eighth subgenus HYMENANTHES, in which the node is complex. Apart from the section CHONIASTRUM which will be considered presently, the distinction between simple and complex nodes presents no real problems. It is true that some leaf traces of the subsection MADDENIA divide in the cortex as they pass into the petiole but accessories are not developed in this group. Similarly, in some species of section VIREYA the leaf trace divides in the cortex, and in addition in this section accessory bundles may occur in the petiole. On the other hand, in the few members of HYMENANTHES which lack accessory bundles, the leaf trace is divided in the cortex in the manner typical of that subgenus. These aberrant forms are closely related to species with nodes of the typical Complex Unilacunar form. That is to say, most species of the subsection TALIENSIA, for instance, are complex, though one of its species lacks accessory bundles. It is concluded, therefore, that these instances of approach between the two types are secondary modifications resulting from convergent evolution.

The Intermediate Node, found in the section CHONIASTRUM, is possibly nearer to the simple than to the complex node since the central strand, though divided, does not lose the compactness of form characteristic of the simple type. Therefore, it is probably correct to regard it as a modification of that form, though sufficiently distinctive to be considered a separate nodal type.

The other three sections of AZALEASTRUM, namely CANDIDASTRUM, MUMEAZALEA and EUAZALEASTRUM were found to share certain features which contrast strongly with those of CHONIASTRUM. They all bear minute, often strongly curved, simple hairs on the petiole; the petiolar strand is fan shaped in section, not incurved; and some species (e.g. *R. semibarbatum* and *R. ovatum*) have serrated leaf margins. It is suggested that the subgenus AZALEASTRUM might well be subdivided in

order to accentuate the evident close relationship of these three sections, and their equally evident lack of relationship to CHONIASTRUM.

It is probable that a close study of the histology of the nodes and petioles of the azaleas (subgenera PENTANTHERA and TSUTSUTSI) would reveal characters distinguishing them from the nodes of scale-bearing rhododendrons. While it was noticed that branches of the central trace were not infrequent in azaleas but very rare in lepidote species, no diagnostic feature was recorded.

It will be clear from the foregoing discussion that the node offers a character of taxonomic importance. The coincidence between nodal types and the major subdivisions recognized within the genus is striking. That a completely new set of characters indicates groups that accord with existing classification is encouraging, and the validity of the groups is strengthened by this new evidence. The classification of the genus is at present in a transitional state. On the one hand there is an old-established classification in traditional botanical form. This may be seen, for example, in Rehder (1902), where major subdivisions of the genus are defined. This system has the grave practical disadvantage that most of the species, including the majority of interest to horticulturists, fall within two of the major groups. It was for this reason, no doubt, that an empirical, informal classification into series was adopted in *The Species of Rhododendron* (Stevenson, 1930). These series form the most comprehensive and discriminating grouping of the temperate species yet devised. However, the already established major subdivisions of the genus were not employed, the series being presented in alphabetical sequence. A much clearer appreciation of the genus results if the systems are united, giving the advantages of both. This was done by Sleumer in 1949.

While we wish to emphasize this close correspondence between nodal anatomy and classification, we would also draw attention to the interesting variation in detail to be found between members of taxonomic groups, both large and small, between the nodes of different categories of appendages, and between nodes of the same order within one individual. Clearly, the adult anatomy of a node may vary, particularly in some species and some subsections. Nevertheless, the range of variation is limited so that the definition of the major types remains clear, with very few exceptions. The interest of these exceptions must not be allowed to detract from the taxonomic significance of the nodal types which is based on the vast majority of the species.

The anatomical evidence presented here reinforces the view that major groupings are present within the genus. Indeed it provides further evidence for those who would raise these groups to generic rank (Copeland, 1943). The distinctness of the subgenus HYMENANTHES from the remaining groups is suggested by nodal anatomy. It is reinforced by the absence of scales, though this feature is also lacking in several groups with simple nodes. These same groups (azaleas and *Azaleastrum*), moreover, resemble subgenus HYMENANTHES in the aestivation of their foliage leaves (Sinclair, 1937). By employing these three anatomical features in com-

bination, three major subdivisions can be defined (TABLE 3). However, the definition of the resulting groups, whether by anatomy or by external features, such as the position of flower and foliage buds, is complex. For this reason, and also in view of the long horticultural history of the genus, there appears to be little advantage in maintaining separate genera.

TABLE 3

SUBGENUS	ANATOMICAL FEATURES
PENTANTHERA TSUTSUTSI AZALEASTRUM	node simple scales absent aestivation revolute
HYMENANTHES	node complex scales absent aestivation revolute
RHODODENDRON PSEUDAZALEA RHODORASTRUM PSEUDORHODORASTRUM	node simple scales present aestivation convolute (except in subsect. EDGEWORTHIA)

The prevalence of the unilacunar node in so many genera of the Ericaceae suggests that this state is basic for the family and that the comparatively few species with trilacunar nodes in *Rhododendron* are derived from the simpler type. Indeed, the unilacunar node has come to be regarded as primitive for the dicotyledons as a whole, and there are convincing instances of the derivation within a family of trilacunar nodes from the unilacunar condition (Bailey, 1956). This view is supported in *Rhododendron* by the occurrence of two forms of trilacunar node, that occurring in the subsection BARBATA and that in other groups. Kingdon-Ward (1947) adopts the view that the lepidote rhododendrons are primitive and this would imply that the simple node is the original type. On the other hand, Hutchinson (1946) postulates that the subsection FALCONERA resembles the ancestral form of the genus. This group is predominantly trilacunar. Hutchinson's opinion is based on his belief in a resemblance between the subsection FALCONERA and the Dilleniaceae, a family which he considered to be ancestral to the Ericaceae. The node in the principal subfamily of the Dilleniaceae is tri- or pentalacunar (Sinnott, 1914). In *Actinidia* and *Saurauia*, representing the other two subfamilies, the node is unilacunar. Since the majority of dicotyledonous families are characteristically trilacunar, the presence of this nodal type in two groups does not necessarily imply relationship. However, if the Ericaceae are, in fact, derived from the Dillenioideae, the trilacunar node is likely to be the original state in the family. In that event, the genus *Rhododendron* would be primitive within the Ericaceae, as only in this genus are trilacunar nodes known to occur. It must be emphasized that the opinions of Kingdon-Ward and Hutchinson are both speculative. While it is necessary to examine them in the light of the evidence relating to nodal anatomy, no final conclusion can be drawn.

Money, Bailey and Swamy (1950) have suggested that single arc-shaped leaf traces may in fact sometimes represent several concrescent strands. If the more complex type of node were primitive in *Rhododendron*, the very prevalent simple leaf trace which is characteristic of other genera in the family, would be of such a concrescent type.

In this investigation we have observed the node of a little more than one quarter of the species of the genus. A larger sample would undoubtedly have revealed greater variation in some groups. The types described are based on features of vascular patterns. Future studies will include histological characters, and preliminary observations suggest that these additional characters will allow differences between groups with simple traces to be recognized and also that distinct types of node and petiole will be found within the subgenus HYMENANTHES.

SUMMARY

1. The anatomy of the nodes of the mature foliage leaf has been investigated in 264 species of the genus *Rhododendron*. These are presented as falling into five types:

(i) *Simple Unilacunar*: the leaf receives a single trace; rarely, accessory bundles may be present in the petiole.

(ii) *Intermediate*: the trace, while in the cortex, consists of a few bundles closely aggregated into a central cylinder. In the petiole these bundles unite to form a central strand which is accompanied by two or more accessory bundles.

(iii) *Three-trace Unilacunar*: a single arc diverges from the stele before dividing into three separate strands. This division may be in the cortex or just outside the abscission layer.

(iv) *Complex Unilacunar*: several traces arise from a single gap and enter the petiole, where they unite to form a central strand which is accompanied by two or more accessory bundles.

(v) *Complex Trilacunar*: the pattern of traces is similar to type iv, but additional traces leave the stele by separate gaps.

2. Variations are recorded within the framework of these types as they occur in taxa and individuals.

3. The essential features of the Complex Trilacunar Node were found to be established very early in the development of seedlings.

4. All types, including the most complex, pass through a stage of development when only one leaf trace is present.

5. The nodes of cotyledons, cataphylls and perulae are unilacunar even in species with trilacunar foliage leaves.

6. The significance of these findings is discussed in relation to the taxonomic subdivision of the genus.

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SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
SUBGENUS	SECTION	SUBSECTION	SERIES	SUBSERIES		
(EXCLUDED)	—	—	Camtschaticum	—	*camtschaticum* Pallas	
PENTANTHERA	RHODORA	—	Azalea	Canadense	*albrechtii* Maxim.	*vaseyi* A. Gray
	VISCIDULA	—		Nipponicum	*nipponicum* Matsuma	
	PENTANTHERA	—		Luteum	*luteum* Sweet	*occidentale* A. Gray
					roseum (Loisel.) Rehd.	
TSUTSUTSI	BRACHYCALYX	—		Schlippenbachii	*schlippenbachii* Maxim.	
	TSUTSUTSI	—		Obtusum	*kaempferi* Planch.	*yedoense* Maxim.
	TSUSIOPSIS	—		Tashiroi	*tashiroi* Maxim.	
AZALEASTRUM	CANDIDASTRUM	—	Albiflorum	—	*albiflorum* Hook.	
	MUMEAZALEA	—	Semibarbatum	—	*semibarbatum* Maxim.	
	CHONIASTRUM	—	Stamineum	—	*cavaleriei* Lévl.	*esquirolii* Lévl.
					hancockii Hemsl.	*henryi* Hance
					latoucheae Franch.	*oxyphyllum* Franch.
					moulmainense Hook.	*stamineum* Franch.
	EUAZALEASTRUM	—	Ovatum	—	*leptothrium* Balf. f. & Forrest	*ovatum* Planch.
HYMENANTHES	—	AURICULATA	Auriculatum	—	*auriculatum* Hemsl.	
			Griersonianum	—	*griersonianum* Balf. f. & Forrest	
		BARBATA	Barbatum	Barbatum	*argipeplum* Balf. f. & Cooper	*barbatum* Wall.
					smithii Nutt. ex Hook.	
				Glischrum	*erosum* Cowan	*exasperatum* Tagg
					glischroides Tagg & Forrest	*glischrum* Balf. f. & W.W. Sm.
					habrotrichum Balf. f. & W.W. Sm.	
				Crinigerum	*bainbridgeanum* Tagg & Forrest	*crinigerum* Franch.
	MACULIFERA			Maculiferum	*longesquamatum* C. K. Schneid.	*monosematum* Hutch.
					morii Hayata	*pachytrichum* Franch.
					strigillosum Franch.	
	ARBOREA		Arboreum	Arboreum	*arboreum* Smith	*delavayi* Franch.
					niveum Hook. f.	*zeylanicum* Hort. ex Loud.
	ARGYROPHYLLA		) Argyrophyllum		*argyrophyllum* Franch.	*insigne* Hemsl. & Wils.
	FLORIBUNDA		)		*floribundum* Franch.	*hunnewellianum* Rehd. & Wils.
	THOMSONIA		Thomsonii	Thomsonii	*cyanocarpum* (Franch.) W.W. Sm.	*eclecteum* Balf. f. & Forrest
					hookeri Nutt.	*stewartianum* Diels
					thomsonii Hook. f.	*viscidifolium* Davidian
				Cerasinum	*cerasinum* Tagg	
	SELENSIA		) Selense		*selense* Franch.	*dasycladum* Balf. f. & W.W. Sm.
	MARTINIANA		)		*eurysiphon* Tagg & Forrest	*martinianum* Balf. f. & Forrest
	CAMPYLOCARPA		Campylocarpum		*callimorphum* Balf. f. & W.W. Sm.	*caloxanthum* Balf. f. & Farrer
					campylocarpum Hook f.	*telopeum* Balf. f. & Forrest
	SOULIEA		Souliei		*litiense* Balf. f. & Forrest	*souliei* Franch.
					wardii W.W. Sm.	
			Williamsianum		*williamsianum* Rehd. & Wils.	
	IRRORATA		Irroratum	Irroratum	*aberconwayi* Cowan	*eritimum* Balf. f. & W.W. Sm.
					irroratum Franch.	*pankimense* Cowan & Ward
					wrayi King & Gamble	

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
SUBGENUS	SECTION	SUBSECTION	SERIES	SUBSERIES		
		PARISHIA		Parishii	*cookeianum* Davidian	*elliottii* Watt. ex W.W. Sm.
					venator Tagg	
		LACTEA	Lacteum	—	*beesianum* Diels	*lacteum* Franch.
					phaeochrysum Balf. f. & W.W. Sm.	*przewalskii* Maxim.
					traillianum Forrest & W.W. Sm.	*wightii* Hook. f.
		FALCONERA	Falconeri	—	*arizelum* Balf. f. & Forrest	*basilicum* Balf. f. & W.W. Sm.
					coriaceum Franch.	*eximeum* Nutt.
					falconeri Hook. f.	*fictolacteum* Balf. f.
					hodgsonii Hook. f.	*rex* Lévl.
		GRANDIA	Grande	—	*coryphaeum* Balf. f. & Forrest	*grande* Wight
					macabeanum Watt ex Balf. f.	*magnificum* Ward
					praestans Balf. f. & W.W. Sm.	*sidereum* Balf. f.
					sinogrande Balf. f. & W.W. Sm.	
		FULVA	Fulvum	—	*fulvum* Balf. f. & W.W. Sm.	*uvarifolium* Diels
		CAMPANULATA	Campanulatum	—	*campanulatum* D. Don	*fulgens* Hook. f.
					lanatum Hook. f.	*sherriffii* Cowan
					succothii Davidian	*tsariense* Cowan
		TALIENSIA	Taliense	Adenogynum	*bureavii* Franch.	*detonsum* Balf. f. & Forrest
				Roxieanum	*gymnocarpum* Balf. f. & Tagg	*pronum* Tagg & Forrest
					roxieanum Forrest	
				Taliense	*sphaeroblastum* Balf. f. & Forrest	
				Wasonii	*inopinum* Balf. f.	*rufum* Batal.
		NERIIFLORA	Neriiflorum	Forrestii	*chamae-thomsonii* (Tagg & Forrest) Cowan & Davidian	*forrestii* Balf. f. ex Diels
				Haematodes	*chaetomallum* Balf. f. & Forrest	*haematodes* Franch.
					mallotum Balf. f. & Ward	
				Neriiflorum	*neriiflorum* Franch.	*sperabile* Balf. f. & Farrer
				Sanguineum	*aperantum* Balf. f. & Ward	*dichroanthum* Diels
					sanguineum Franch.	
		PONTICA	Ponticum	Caucasicum	*degronianum* Carriere	*hyperythrum* Hayata
					makinoi Tagg	*ungernii* Trautv.
					yakusimanum Nakai	
				Ponticum	*catawbiense* Michaux	*macrophyllum* D. Don
					ponticum L.	
		FORTUNEA	Fortunei	Calophytum	*calophytum* Franch.	
				Davidii	*planetum* Balf. f.	*praevernum* Hutch.
					sutchuenense Franch.	
				Fortunei	*decorum* Franch.	*diaprepes* Balf. f. & W.W. Sm.
					discolor Franch.	*fortunei* Lindl.
					vernicosum Franch.	
				Orbiculare	*orbiculare* Decaisne	
				Griffithianum	*griffithianum* Wight	
				Oreodoxa	*fargesii* Franch.	*oreodoxa* Franch.

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
SUBGENUS	SECTION	SUBSECTION	SERIES	SUBSERIES		
PSEUDAZALEA	—	—	Trichocladum	—	*chloranthum* Balf. f. & Forrest	*lepidostylum* Balf. f. & Forrest
					melinanthum Balf. f. & Ward	*trichocladum* Franch.
RHODORASTRUM	—	—	Dauricum	—	*dauricum* L.	*mucronulatum* Turcz.
PSEUDORHODORASTRUM	TRACHYRHODION	—	Scabrifolium	—	*mollicomum* Balf. f. & W.W. Sm.	*pubescens* Balf. f. & Forrest
					scabrifolium Franch.	*spiciferum* Franch.
	RHODOBOTRYS	—			*racemosum* Franch.	
	RHABDORHODION	—	Virgatum	—	*virgatum* Hook. f.	
RHODODENDRON	LEPIPHERUM	CAMELLIAEFLORA	Camelliaeflorum		*camelliaeflorum* Hook. f.	
		BOOTHIA	Boothii	Boothii	*chrysodoron* Tagg ex Hutch.	*sulfureum* Franch.
				Megeratum	*leucaspis* Tagg	*megeratum* Balf. f. & Forrest
		TEPHROPEPLA		Tephropeplum	*auritum* Tagg	*tephropeplum* Balf. f. & Farrer
					xanthostephanum Merr.	
		EDGEWORTHIA	Edgeworthii	—	*edgeworthii* Hook. f.	*pendulum* Hook. f.
		GLAUCA	Glaucophyllum	Glaucophyllum	*brachyanthum* Franch.	*charitopes* Balf. f. & Farrer
					glaucophyllum Rehd.	*tsangpoense* Hutch. & Ward
		GENESTERIANA	Maddenii	Genesterianum	*genesterianum* Forrest	
		MADDENIA		Ciliicalyx	*burmanicum* Hutch.	*ciliatum* Hook. f.
					ciliicalyx Franch.	*formosum* Wall.
					johnstoneanum Watt	*scopulorum* Hutch.
					valentinianum Forrest	*veitchianum* Hook.
				Maddenii	*crassum* Franch.	*maddenii* Hook. f.
				Megacalyx	*lindleyi* Moore	*megacalyx* Balf. f. & Ward
					nuttallii Booth	*taggianum* Hutch.
		MOUPINENSIA	Moupinense	—	*moupinense* Franch.	
		SALUENENSIA	Saluenense	—	*calostrotum* Balf. f. & Ward	*keleticum* Balf. f. & Forrest
					nitens Hutch.	*radicans* Balf. f. & Forrest
					saluenense Franch.	
		TRIFLORA	Triflorum	Augustinii	*augustinii* Hemsl.	
				Hanceanum	*hanceanum* Hemsl.	
				Triflorum	*ambiguum* Hemsl.	*bauhiniiflorum* Watt ex Hutch.
					lutescens Franch.	*triflorum* Hook. f.
				Yunnanense	*concinnum* Hemsl.	*davidsonianum* Rehd. & Wils.
					oreotrephes W.W. Sm.	*yunnanense* Franch.
		CAMPYLOGYNA	Campylogynum	—	*campylogynum* Franch.	
		CAROLINIANA	Carolinianum	—	*carolinianum* Rehd.	*minus* Michaux
					chapmanii A. Gray	
		FERRUGINEA	Ferrugineum	—	*ferrugineum* L.	*kotschyi* Simonk.
		HELIOLEPIDA	Heliolepis	—	*desquamatum* Balf. f. & Forrest	*heliolepis* Franch.
					rubiginosum Franch.	
		LAPPONICA	Lapponicum	—	*edgarianum* Rehd. & Wils.	*fastigiatum* Franch.
					flavidum Franch.	*hippophaeoides* Balf. f. & W.W. Sm.
					idoneum Balf. f. & W.W. Sm.	*microleucum* Hutch.
					russatum Balf. f. & Forrest	
		MICRANTHA	Micranthum	—	*micranthum* Turcz.	
		CINNABARINA	Cinnabarinum	—	*cinnabarinum* Hook. f.	*concatenans* Hutch.
					keysii Nutt.	*xanthocodon* Hutch.
		LEPIDOTA	Lepidotum	Lepidotum	*lepidotum* Wall.	
		BAILEYA		Baileyi	*baileyi* Balf. f.	
		UNIFLORA	Uniflorum	—	*ludlowii* Cowan	*patulum* Ward
					pemakoense Ward	*uniflorum* Hutch. & Ward

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
SUBGENUS	SECTION	SUBSECTION	SERIES	SUBSERIES		
	POGONANTHUM	—	Anthopogon	—	*anthopogon* D. Don	*cephalanthum* Franch.
					sargentianum Rehd. & Wils.	*trichostomum* Franch.
	VIREYA		Vaccinioides			
		PSEUDOVIREYA			*invasiorum* Sleum.	*perakense* King & Gamble
					saruwagedicum Foerster	*seimundii* J.J. Smith
					spathulatum Ridl.	*vaccinioides* Hook. f.
		SIPHONOVIREYA			*herzogii* Warb.	
		PHAEOVIREYA			*beyerinkianum* Koord.	*konori* Becc.
					superbum Sleum.	
		MALAYOVIREYA			*malayanum* Jack	*vinicolor* Sleum.
		ALBOVIREYA			*yelliottii* Warb.	
		SOLENOVIREYA			*jasminiflorum* Hook.	*pleianthum* Sleum.
		EUVIREYA				
		SERIES				
		Linnaeoides			*gracilentum* F. v. Muell.	
		Saxifragoides			*saxifragoides* J.J. Smith	
		Taxifolia			*taxifolium* Merr.	
		Stenophylla			*purpureiflorum* J.J. Smith	
		Citrina			*citrinum* (Hassk.) Hassk.	
		Buxifolia			*commonae* Foerster	*pauciflorum* King & Gamble
					luteosquamatum Sleum.	
		Javanica			*brookeanum* Low ex Lindl.	*culminicolum* F. v. Muell.
					javanicum (Bl.) Benn.	*intranervatum* Sleum.
					lochae F. v. Muell.	*laetum* J.J. Smith
					macgregoriae F. v. Muell.	*leucogigas* Sleum.
						longiflorum Lindl.
						robinsonii Ridl.

A NEW HYDRANGEA FROM MEXICO

Lorin I. Nevling, Jr., and Arturo Gómez-Pompa

THE GENUS *Hydrangea* is familar to both layman and scientist primarily through species which have ornamental value. Since the species most widely cultivated are shrubby, with the exception of the spectacular climbing *H. anomala* D. Don, and usually have been selected for inflorescences bearing large numbers of sterile flowers, one tends to have a distorted impression of the genus as a whole. In the recent monograph by Elizabeth McClintock (1957) two sections were recognized: HYDRANGEA and CORNIDIA, containing 11 and 12 species respectively. Section HYDRANGEA includes most of the cultivated species, all of which are shrubs, excepting *H. anomala*. Two species of this group, *H. arborescens* L. and *H. quercifolia* Bartram, are native to the southeastern United States, the remainder are Asiatic. In contrast, species of section CORNIDIA seem to be more flexible in growth form with many species occurring both as shrubs and climbers, depending on circumstances of position and, perhaps, age. The normal mature form, however, is a root climber. The species of this section are native to the New World, excepting *H. integrifolia* Hayata of Formosa and the Philippines. Thus 13 of 23 species are climbers.

In this paper a new climbing species of section CORNIDIA is described as *Hydrangea nebulicola* (FIGS. 1 and 2). It was discovered in the deciduous liquidambar-oak forest of the Sierra de Chiconquiaco north of Jalapa, Veracruz, México. This zone can be characterized floristically by the abundance of individuals of *Alnus, Clethra, Cyathea, Hedyosmum, Liquidambar, Magnolia, Meliosma, Podocarpus,* and *Quercus* (see Gómez-Pompa, 1966). The climate in this region is temperate due to altitude (ca. 1500 m.) and extremely humid, not only because of high rainfall (250–300 cm. annually), but also because of the many clouds which sweep through the forest. It is difficult to determine the temperature in this zone exactly. However, from data obtained from a climatological station nearby (Naolinco, Ver.) we are able to give a mean temperature of between 17° and 18° C. The coldest month is January with an average of 12° to 14° C, the extreme minimum temperatures during this period being some degrees below 0° C. The topography is rather rugged with slopes of 10 to 40 percent. The soil, which is derived from volcanic rock, contains abundant organic matter. The new species is abundant only locally, and it possesses several characteristics which we believe to be of important evolutionary significance within the genus and which mark it as a very specialized member of section CORNIDIA. One of the most interesting aspects of this species is its vegetative reproduction. We believe that this type of reproduction has an adaptive value sufficient for the species even though the scarcity of individuals is notable. Several trips have been made without

FIG. 1. *Hydrangea nebulicola*. (*Gómez-Pompa 1541*). Flowering branch with details of inflorescence and pubescence of lower leaf-surface.

success to search for pistillate specimens. All that we have observed is that the flowering of the species is rare although it may continue over several months. With these considerations in mind and the realization that the species is both rare and dioecious we can understand the importance of vegetative reproduction and its rôle in survival.

In climbing species of this genus, three kinds of shoots are generally found: juvenile, found only in young plants; the terminal one, which functions as a climbing shoot; and the lateral shoot, which supports the reproductive functions and the primary photosynthetic activity. When a tree is the substrate the climbing often is restricted to a single individual. In this new *Hydrangea* several deviations from the general ground plan just mentioned are to be found. Although no juvenile plants were located in spite of a careful search, a fourth type of shoot bearing a marked re-

FIG. 2. Flowering branch of *Hydrangea nebulicola* showing paired inflorescences at anthesis and young inflorescences enclosed by cucullate bracts. Photograph from *Nevling & Gómez-Pompa 39*.

semblance to juvenile shoots was found. These, termed runner-shoots, were discovered along the forest floor, sometimes covered by leaf-litter. They permit a single plant to climb several individual trees simultaneously. Runner-shoots (FIG. 3) were quite common and are characterized morphologically by reduced bract-like deciduous leaves and adventitious roots on the lower and lateral surfaces, similar in external appearance to those found in *Hedera helix* L. These peculiar shoots seem to be selective as to the substrate tree, for they were found ascending only relatively mature tree trunks, although no selection as to substrate species is obvious. As a runner-shoot begins an ascent the reduced leaves become larger with a few marginal serrations above the middle of the lamina but very soon become similar to the mature leaf in form and size. The climbing shoot (FIG. 3) is characterized by a very marked unequal production of secondary xylem, the mass of the new wood being produced in the direction of the substrate. This apparently permits the continuing production of the adventitious roots necessary for attachment to the substrate. It is believed that detailed comparison of the wood anatomy of climbing *vs.* non-climbing species of *Hydrangea* might prove useful in the determination of evolutionary direction within the genus.

The inflorescences of species of *Hydrangea* are marked by having either monomorphic or dimorphic flowers. These two conditions are denoted by students of the genus as fertile and sterile flowers: fertile flowers being bisexual with androecium and gynoecium normally developed; sterile